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Phylogeny of the Hawaiian Species of the Genus *Lepidocyrtus* (Collembola, Entomobryidae)*

BY

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Synopsis: We made a phylogenetic analysis of the 15 endemic species of Hawaiian *Lepidocyrtus* (S.L.) using PHYLIP. We discovered that several characteristics viz: basal knobs or lobes on the dens and truncate empodial appendages have been evolved and/or lost on the islands. The use of such characteristics for supraspecific separation into such genera as *Ascocyrtus* and *Acrocyrtus* is thus very questionable.

Keywords: Collembola, *Lepidocyrtus*, Hawaii, Phylogeny.

INTRODUCTION

During our soon to be published Collembola of Hawaii study we discovered that the genus *Lepidocyrtus* contained 17 endemic and 2 non-endemic (hereinafter called exemic) species. The presence of the large number of endemic species afforded us an opportunity of studying groups of species of this genus with some degree of certainty that we were examining monophyletic groups. We determined a wide variety of characteristics on these species (*see* Tab. I).

We used these characteristics to analyze the phylogeny of the Hawaiian species using the various programs of PHYLIP made available by J. FELSENSTEIN (1990) of the University of Washington. We were unable to use two endemic species for this analysis. *L. heteropthalmus* is apparently extinct and we saw only 1 poorly preserved type specimen. *L. sp. Y* which did not display many features. The remaining species were examined in detail.

* This article has been written *in memoriam* Claude DELAMARE DEBOUTTEVILLE, one of soil zoology founders.

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I. – METHODS

We used all of the data presented in Table I in our analyses. Since PHYLIP requires binary data we changed all multistate characters into series of binary state characteristics. This transformation resulted in a Table of 16 species and 39 characteristics.

There was no *a priori* reason for weighting any characteristic more heavily than another or for assuming that there was a universal polarity in the various states for any characteristic; therefore, initial analyses created unrooted Wagner trees using the PENNY program and WAGNER option. We also ran CLIQUE programs to determine characteristics which could have been uniquely evolved and used these characteristics to determine phylogenetic trees. On a basis of repeated patterns seen in many different phylogenies we ran MIX options with the PENNY program where we assumed that bilobed antennal bulbs derived from unlobed bulbs, and that truncate unguiculi derived from acuminate ones and that scaled antennae and legs derived from unscaled forms. We also ran DOLPENNY programs which allowed us to treat the above changes not as certainly but probably unidirectional. We added to these features some of the chaetotaxy features where we treated the loss of setae as more probable than the gain of setae and reduction or smoothness of labial setae and the presence of dental tubercles as more likely to be derived states than primitive states to see how phylogenies derived from such analyses would differ from those using WAGNER trees. In all cases we used the CONSENSE program to establish a consensus phylogeny from the various trees thus obtained.

II. – RESULTS

In all programs it seemed very likely that the two exemic species, were not related to the endemic species. The exemic species either appeared to be more closely related to each other than any other species or apomorphic species which had been evolved on the islands. The latter seemed highly improbable and thus we removed *violaceus* and *pallidus* from further phylogenetic analyses. The discussion below is limited to the 14 endemic species for which we had adequate information for analysis.

In all programs it soon became clear that one group, consisting of the five endemic species: *E*, *EE*, *T*, *W*, and *inornatus* are a tightly knit group and very discrete from most other species (see *Fig.* 1). In almost all programs two other species. *C* and*Z*, were also associated with these six. We shall call this group lineage **A**. All seven have apical antennal bulbs but are quite varied in other characteristics.

Figure 2 shows the results of the phylogenetic analysis of the lineage **A** species using the MIX option described above. The primitive features are those seen in *L.* sp. *E* (*see* Tab. I). The changes which occur are indicated in figure 2 at the level shown. If the program is run with all characteristics there is only a single most parismonious tree and it is unrooted. When other phylogenies were developed for these species using the other methods described earlier, there was remarkable consistency of phylogeny for all programs. We used all of the options described above but essentially the same tree was obtained in every case. The differences under different assumptions affected only two species. Species *C.* was separated from the other species when the DOLPENNY assumptions were used. Species *Z.* varied in the postion where it branched away from species *E.* and *W.* As a result we feel a high degree of confidence that this is a monophyletic group which has evolved in Hawaii. The only possible exception is sp. *Z* which is both quite distinct

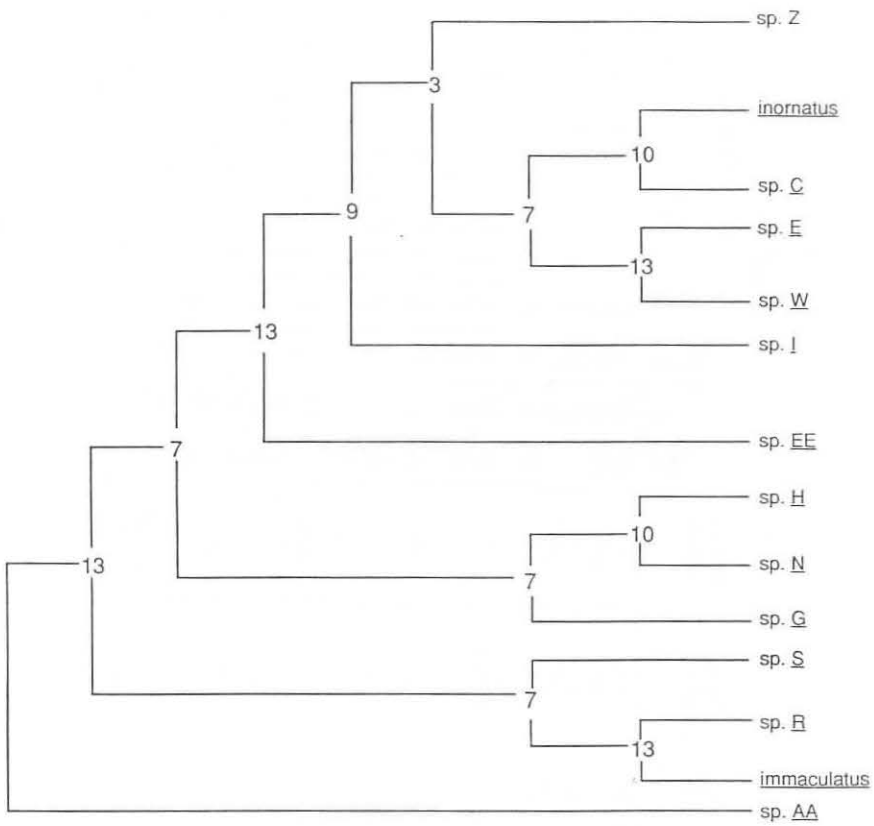

FIG. 1. – Unrooted Wagner consensus tree for the endemic species of Hawaiian *Lepidocyrtus*. The numbers at the forks indicate the number of times the group consisting of the species which are to the right of that fork occured among the 13 trees found.

from the others and inconsistent in its position on the different phylogentic trees. The ancestor of lineage **A** is unknown as is lineage **A**'s possible source region.

The analysis of the remaining species, which we shall call the lineage **B** species, also showed clearly that the two species were probably not related to any of the endemic species. The phylogenies produced by the various methods described above were not as consistent as those seen with lineage **A**. If we use *violaceus* as an outgroup, or rely on any rooted phylogenies using Wagner trees, *L.* sp. *AA* appears to be the basal species. Programs creating Wagner trees, using either characteristics which are shown to be potentially uniquely evolved, or all characteristics, came out very similar to the tree shown in Figure 3. On the other hand programs, using the MIX option of PENNY as described above or the DOLPENNY, produce trees similar to that seen in Figure 4. We do not see any clear basis for choosing between these phylogenies at the present time.

TAB. I. — **Characteristics of Hawaiian Species of *Lepidocyrtus***

Species	Color	Apical antennal bulb	Cephalic *diagonal* antennal	Eye G/F	Ungui culus	Dental tubercle	Chaetotaxy								
							Labium					Dorsum of head			
							M	M	R	E	L	R_2	S	T	Po
sp. *AA*	blue	–	1.25-1.40	≈	ac	–	*M*	*M*	vq	*E*	*L*	–	–	–	+
sp. *C*	blue	bilobed	10/13-4/6	≈	ac	small	(*m*)	*M*	vg	*E*	*L*	–	–	–	–
sp. *E*	blue	+	8/11	≈	ac	–	–	*M*	vg	*E*	*L*	+	–	–	+
sp. *EE*	blue	+	5/8	< ≈	ac	+	–	*M*	vg	*E*	*L*	–	–	–	–
sp. *G*	blue	–	8/11	≪	tr	+	*M*	*M*	vg	*E*	*L*	±	±	–	+
sp. *H*	yellow blue	–	5/7	< ≈	ac weakly tr	+	*M*	*M*	*r*	*E*	*L*	+	–	–	–
heteropthalmus		+	1.00	≪	ac	++	*M*	M	*R*	E	L	?	?	?	?
sp. *N*	blue yellow	–	12/15-8/14	≪	tr	+	*M*	*M*	*R*	*E*	*L*	+	+	–	–
immaculatus	yellow blue	–	13/24	< ≈	tr	++	m M *m*	M	vg	E	L	–	–	–	–
inornatus	blue-yellow	+	4/5	≈	ac	small	–	M	vg	E	*L*	+	–	–	–
pallidus	blue	–	5/7	<	ac	–	*M*	*M*	o	*E*	*L*	–	–	+	–
sp. *R*	yellow	–	7/9-7/11	<	tr	–	*M*	M	*R*	E	L	–	–	–	–
sp. *S*	blue	–	7/11-7/12	≪	ac	–	*M*	*M*	*r*	*E*	*L*	–	–	–	–
sp. *T*	blue	bilobed	7/10	≈	ac	+	–	*M*	vg	*E*	*L*	–	–	–	–
violaceus	blue	–	20/23	<	ac	–	*M*	*M*	*R*	*E*	*L*	–	–	–	–
sp. *W*	blue	+	7.5/10	<	ac	–	–	*M*	vg	*E*	L	+	–	–	–
sp. *Y*	blue	–	7/8	<	ac	small	–	*M*	O	*E*	*L*	–	–	–	?
sp. *Z*	yelow	bilobed	4.5/6.5	<	tr	++	*M*	*M*	vg	*E*	*L*	–	–	–	–

TAB. I. – (*continued*).

Species	Chaetotaxy second abdominal segment							Scales antennae hind femur	Third abdominal segment			Fourth abdominal segment			
	SAS	AS	B	*a*	q_1	c_2	*p*		c_1	d_2	d_3	P_1	M	s	post*
sp. *AA*	+	2	*M*	M	+	*M*	+	–	+	+	+ –	–	2	+	0
sp. *C*	+	2	–	m	–	*M*	+	–	–	+	+	–	2	–	0
			M												
sp. *E*	–	3	(m)	*m*	–	*M*	–	–	–	–	+	–	2	+	0
sp. *EE*	+	2	–	m	+	*M*	–	–	+	–	+	–	2	+	0
sp. *G*	+	2	m	m	–	m	+	–	+	+	–	–	3	–	10
sp. *H*	+	2	*m*	m	+	m	–	–	+	+	+	–	3	–	0
heteropthalmus	?	?	?	?	?	?	?	+	?	?	?	–	3	?	?
sp. *N*	+	2	*m*	m	+	m	–	–	–	+	+	–	3	–	0
immaculatus	–	3	*M*	–	–	*M*	–	+	–	+	+	+	3	+	16-22
inornatus	+	2	–	*m*	–	*M*	+	–	–	–	+	–	2	–	10
pallidus	–	3	*M*	–	+	*M*	+	–	–	+	+	+	2	+	8
sp. *R*	–	2	*M*	*m*	–	*M*	+	–	+	+	+	+	3	+	16-22
sp. *S*	+	2	–	m	+	*M*	+	–	–	+	+	+?	2	+	0
sp. *T*	+	2	–	*m*	+	*M*	–	–	+	+	+	–	3	–	0
violaceus	+	1	*M*	m	+	*M*	–	+	+	–	+	+	3	+	10
sp. *W*	–	2	*M*	–	+	*M*	–	–	–	–	–	–	3	+	0
sp. *Y*	?	?	*M*	?	?	?	?	?	?	?	?	–	2	?	0
sp. *Z*	+	1	–	*m*	–	*M*	–	+	+	+	+?	–	2	–	22

ac+acuminate tr=truncate chaetotaxy: capitalized symbols stand for large setae, lower case symbols for small setae; underlined symbols for ciliate setae (others are smooth); vg=vestigial, o or – =absent.

* The large posterior setae on the fourth abdominal segemtn may be hard to make out, and this character should be relied on only if the specimen has relatively complete vestiture. In *L. heterophthalmus*, ciliate microchaetae are found here.

\# Dental tubercle may be confused with dental clasp.

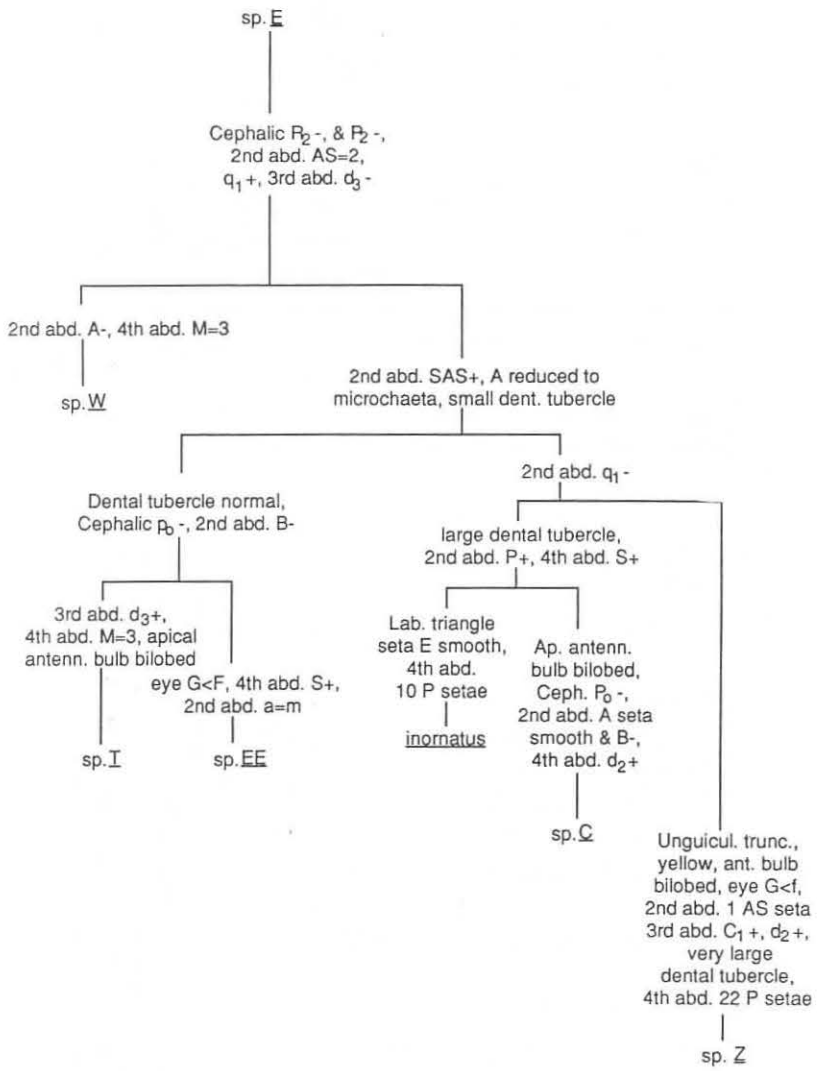

FIG. 2. – Phylogeny of Lineage **A** using PENNY with MIX option (*see* text). Conventions as in Tab. I. Changes taking place where indicated in phylogeny. Relative lengths of vertical lines are equal to morphological distance from ancestor.

III. – DISCUSSION

The data we have examined would strongly support an idea that there were 2 or possibly 3 ancestral introductions which gave rise to the present day endemic species of *Lepidocyrtus*. The third introduction might account for sp. *Z* which seems to be anomalous in many respects; however, it could also be the last survivor of a longer segment of lineage **B** which includes the probably extinct species

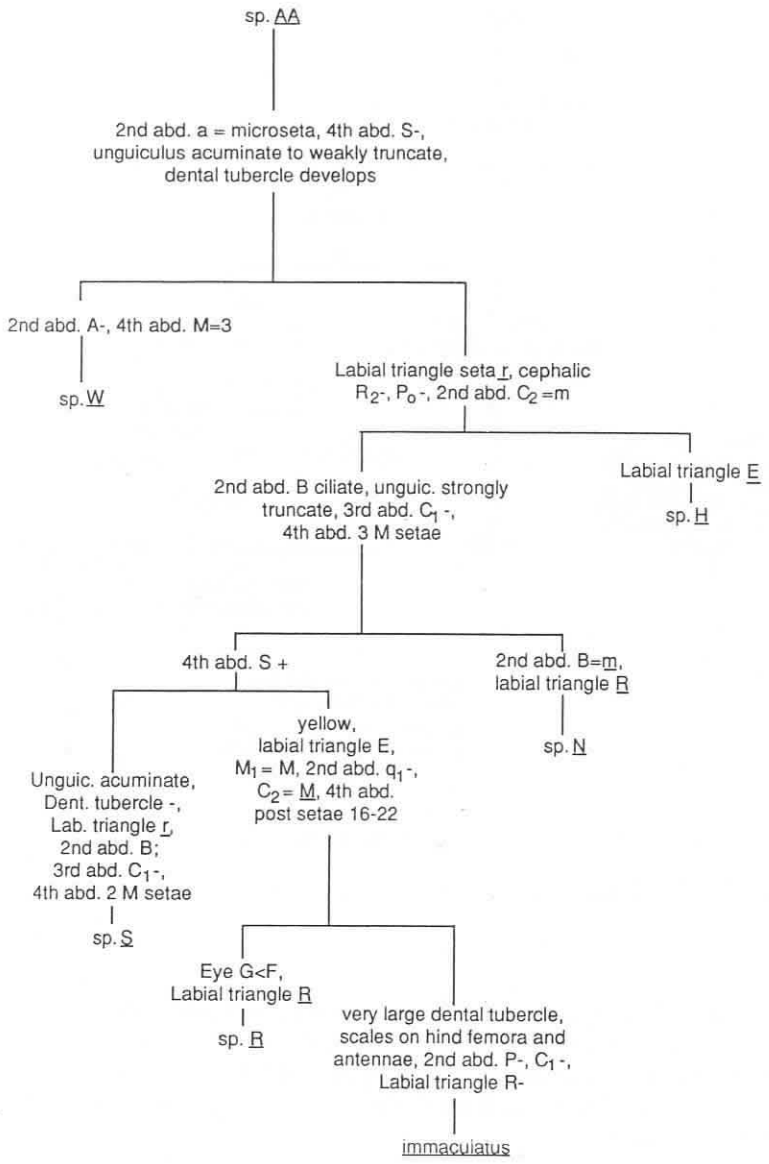
sp. AA
2nd abd. a = microseta, 4th abd. S-, unguiculus acuminate to weakly truncate, dental tubercle develops
2nd abd. A-, 4th abd. M=3
sp. W
Labial triangle seta r, cephalic R2-, Po-, 2nd abd. C2 =m
2nd abd. B ciliate, unguic. strongly truncate, 3rd abd. C1 -, 4th abd. 3 M setae
Labial triangle E
sp. H
4th abd. S +
2nd abd. B=m, labial triangle R
sp. N
yellow, labial triangle E, M1 = M, 2nd abd. q1 -, C2 = M, 4th abd. post setae 16-22
Unguic. acuminate, Dent. tubercle -, Lab. triangle r, 2nd abd. B; 3rd abd. C1 -, 4th abd. 2 M setae
sp. S
Eye G<F, Labial triangle R
sp. R
very large dental tubercle, scales on hind femora and antennae, 2nd abd. P-, C1 -, Labial triangle R-
immaculatus

FIG. 3. – Wagner phylogeny lineage **B** with *ceu* as basal species. Conventions and changes as in figure 2.

heteropthalmus. In either case when we examine the two (or three) lineages we are left with a number of characteristics which are not usable as supraspecific criteria since they are clearly not features distinguishing monophyletic lineages. These include the presence or size of the basal dental knobs and truncate versus acuminate unguiculi. In order for either one of these characteristics to have been monophyletic there would have to have been 5 separate introductions of species ancestral to the

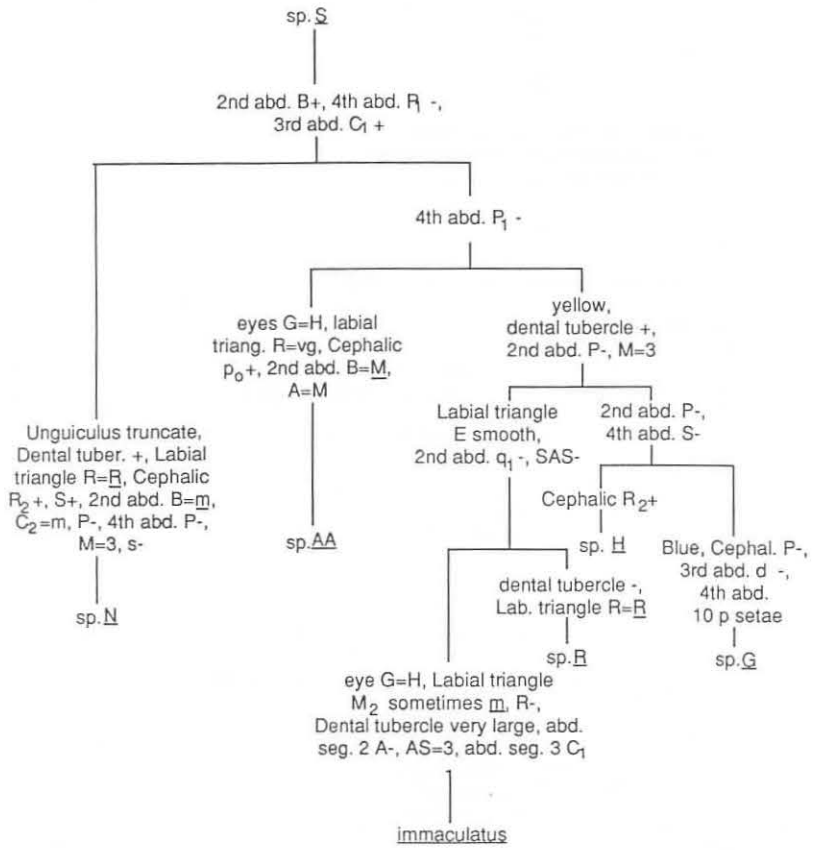
sp. S
2nd abd. B+, 4th abd. R -,
3rd abd. C1 +
4th abd. P1 -
eyes G=H, labial triang. R=vg, Cephalic p0+, 2nd abd. B=M, A=M
yellow, dental tubercle +, 2nd abd. P-, M=3
Unguiculus truncate, Dental tuber. +, Labial triangle R=R, Cephalic R2 +, S+, 2nd abd. B=m, C2=m, P-, 4th abd. P-, M=3, s-
Labial triangle E smooth, 2nd abd. q1 -, SAS-
2nd abd. P-, 4th abd. S-
Cephalic R2+
sp. AA
sp. H
Blue, Cephal. P-, 3rd abd. d -, 4th abd. 10 p setae
dental tubercle -, Lab. triangle R=R
sp. N
sp. R
sp. G
eye G=H, Labial triangle M2 sometimes m, R-, Dental tubercle very large, abd. seg. 2 A-, AS=3, abd. seg. 3 C1
immaculatus

FIG. 4. – Phylogeny of lineage **B** using DOLPENNY. Conventions as in Figure 2.

endemic species of the islands and for both to have occurred there would have to have been 7 introductions, all of these ancestral species now being extinct. The likelihood of this seems minuscule and it would require separation of species which are otherwise very similar to each other on no basis other than *a priori* judgments about interrelationships.

Of all the characteristics we have examined only the presence or absence of an apical antennal bulb appears to have the possibility of separating monophyletic lineages in Hawaii. Certain other features would be useful in separating the lineages but would not be not be diagnostic. These are: Labial setae *r* & *R*, 3rd abdominal segment seta c_1, and 4th abdominal segment seta P_1 which is common in lineage **B** but never present in lineage **A**. Labial eta *R* is vestigial in all of lineage **A** but rarely so in lineage **B** and seta M_1 is *M* in all of lineage **B** but rarely thus in lineage **A**.

IV. – CONCLUSIONS

The changes of features such as basal dental knobs and truncate unguiculi within the limits of clearly monophyletic groups on the Hawaiian islands makes the present supraspecific classification of the genus *Lepidocyrtus* entirely unsatisfactory. It seems to us that the best course of action is to consider all the genera such as *Ascocyrtus* and *Acrocyrtus* which are diagnosed by features such as basal dental tubercles as part of the genus *Lepidocyrtus* until such time as a large scale phylogenetic analysis of the genus can be made.

Acknowledgements

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Résumé

Phylogénie des espèces hawaiiennes du genre *Lepidocyrtus* (Collembola, Entomobryidae)

Nous avons étudié les 18 espèces de *Lepidocyrtus* qui se trouvent dans les îles hawaiiennes. Nous avons pu en analyser la phylogénie pour 16 d'entre elles à l'aide des divers programmes PHYLIP (Felsenstein, 1986). Nous avons découvert que les deux espèces exémiques étaient sans rapport avec les espèces endémiques. Les 14 autres espèces, endémiques, se partageaient nettement en deux lignées, caractérisées par la présence ou l'absence d'une ampoule apicale. L'analyse de ces lignées a montré que les quelques caractères dont on se sert traditionnellement pour séparer les genres ou sous-genres ne peuvent pas être monophylétiques et, en conséquence, doivent être abandonnés pour la reconnaissance des catégories supraspécifiques.

Summary

We studied the 18 species of *Lepidocyrtus* which occur in the Hawaiian islands. We were able to analyze the phylogeny of 16 of these with the aid of the various programs of PHYLIP (Felsenstein, 1986). We discovered that the two exemic species were unrelated to the endemic species. The 14 remaining endemic species clearly fell into two lineages, characterized by the presence or absence of an apical antennal bulb. Analysis of these lineages demonstrated that several characteristics traditionally used to separate genera or subgenera cannot be monophyletic and therefore should be abandoned as justifying supraspecific categories.

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